

POPULATION BIOLOGY AND WING COLOR VARIATION IN *HELICONIUS ERATO PHYLLIS* (NYMPHALIDAE)

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ABSTRACT. Twenty-six months of mark-recapture study of three populations of *Heliconius erato phyllis* in SE Brazil showed these populations to be relatively stable through time. The adults showed high longevity, similar to that of other tropical *Heliconius*. Sex ratio was male biased, and males showed longer residence times than females. The number of red raylets on the ventral hindwing showed seasonal variation, considered to be numeric polyphenism. Of all the species of *Heliconius*, *H. erato* is proposed to be the most tolerant of variation in habitat, larval and adult resources ("ecological plasticity"). These traits are proposed as reasons for the wide distribution of this species in tropical America.

Additional key words: mark-recapture, Heliconiini, Passifloraceae, red raylets, polyphenism.

Even if Heliconiine butterflies are among the best-studied tropical insects, with much known about their systematics, population ecology, behavior, immature biology, host plant relationships, coevolution, mimicry, chemistry, genetics, and conservation (Ehrlich and Gilbert 1973, Brown & Benson 1974, Gilbert 1975, Araujo 1980, Brown 1981, Turner 1981, Sheppard et al. 1985, Mallet 1986a, 1986b), data are not available for most species and geographic populations of *Heliconius*; and generalizations based on other well-known species and regions may fail to explain local patterns and processes. For example, the current idea that *Heliconius* maintain relatively stable population numbers through time (based mainly on Turner 1971 and Ehrlich & Gilbert 1973) is not true for *Heliconius erato phyllis* (F.) near the limits of its range in temperate southern Brazil (Saalfeld & Araujo 1981).

Heliconius erato is the most widespread species of the genus, present in several different habitats and forest types from Mexico to north Argentina (Emsley 1964, 1965), and its subspecies *phyllis* has the widest geographic distribution (Brown 1979, Sheppard et al. 1985) and environmental tolerances (Araujo 1980). In the southern populations of *H. erato* (30°S), periodic variation in several features of wing color pattern, especially the hindwing red-raylets, has also been noted (Pansera & Araujo 1983, Oliveira & Araujo 1992). The present study describes features of a population of *H. erato phyllis* in a subtropical rainforest in southeastern Brazil (24°S), 6° (660 km) farther north of the southern limits of the species distribution, and reports cyclical annual variation in two wing color-pattern elements.

STUDY SITES AND METHODS

A mark-release-recapture (MRR) study was carried out in three areas in São Paulo state, southeastern Brazil. The main study area was "Morro do Voturuá" (MV) (46°22'W, 23°57'S), in the city of São Vicente (Fig. 1). The site was originally covered with lowland subtropical rainforest (Uruahy et al. 1987). The annual rainfall reaches 2500 mm and the average annual temperature is 21°C (Setzer 1949, Prodesan 1969, Nimer 1972), with the mean of the coldest month 18.2°C and of the warmest month 25.3°C (Santos 1965) (Fig. 2, methods following Santos 1965 and Walter 1985). Most of the area is covered by secondary forest on low hills (100–200 m elevation). Similar work was done in two nearby sites: the "Vale do Rio Quilombo" (VQ, Fig. 1), a road along a river valley with much secondary vegetation and flowers, 12 field days over three months; and the "Morro do Japu" (MJ, Fig. 1), a large hill facing the ocean SW of MV with similar vegetation, 47 field days over seven months (see details on these areas in Freitas 1993).

Mark-release-recapture studies were made in Morro do Voturuá during 26 months, from 13 August 1994 to 30 September 1996, 1–4 times per week, totaling 153 field days (about 4 hours/day). Butterflies were captured with an insect net, individually numbered on the underside of both forewings (in the red central macula) with a black permanent felt-tipped pen, and released. Age (based on wing wear), forewing length (in mm), point of capture, sex and food sources were recorded (as in Freitas 1993, 1996). The age of individual butterflies was estimated based on wing wear, initially using the six categories described by

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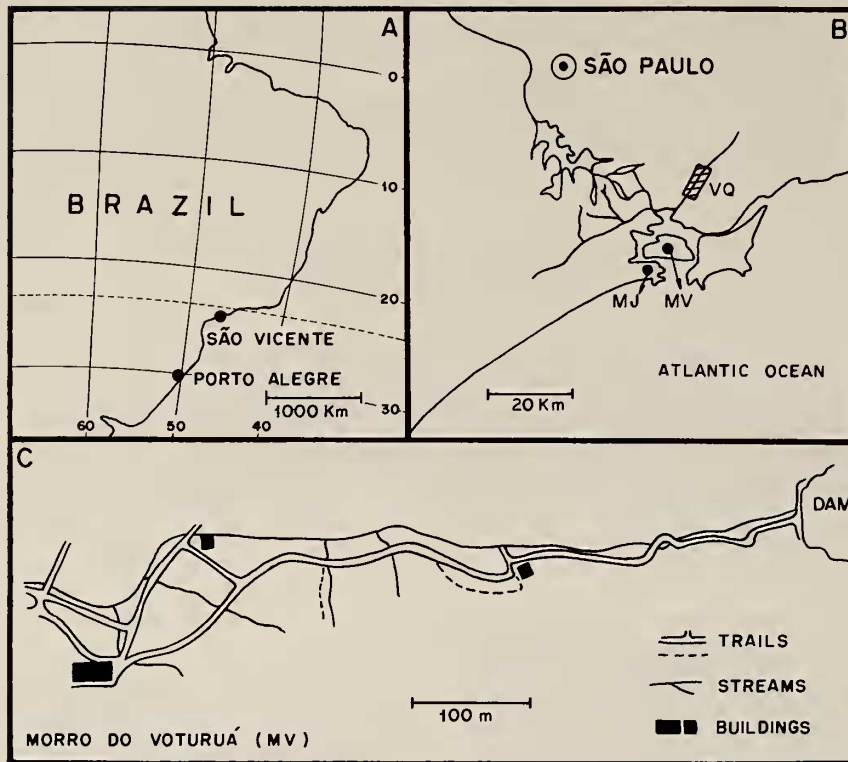


FIG. 1. (A) study area (São Vicente Region) in Southeastern Brazil. In regional map (B), VQ = Vale do Rio Quilombo, MJ = Morro do Japuí, MV = Morro do Voturuá (details in C).

Ehrlich and co-workers (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973). These six categories (freshly emerged, new, intermediate, old, very old, tattered) were regrouped into three categories: new = freshly emerged and new individuals, intermediate = intermediate individuals, and old = old, very old, tattered (as in Freitas 1993, 1996). Age structure was calculated as the daily proportion of each category, and grouped into monthly means. Three wing-color-pattern elements were recorded (Fig. 3): the number of red basal spots, the number and shape of the red raylets on the ventral hindwing, and the color and size of the spot in the inner angle of space Cu1–Cu2 (“cubital spot”) on the dorsal forewing (nomenclature following Miller 1970). Data from August and September 1994 at MV were regarded as the “Winter 1994” sample; each of the following seasons represents observations for 3 consecutive months.

The MRR data from MV were analyzed by the Jolly-Seber method (Southwood 1971) for estimating population parameters (software developed by R. B. Francini, UNISANTOS). In most cases, only males were analyzed because of the low number of females. Daily results were tabulated as “number of individuals captured per day” (NICD), and “number of individu-

als present per day” (NIPD). To estimate the NIPD, recaptured individuals were considered to be present in the population on all previous days since the day of first capture (=marked animals at risk).

RESULTS

Population Dynamics

In Morro do Voturuá, the NICD for males varied from one to 13 (mean = 5.9, SD = 2.4; $n = 153$ days), with 19 days with $n = 3$ and 13 days with $n = 10$ males (Fig. 4). The number of newly marked individuals captured in each month (=monthly recruitment) also varied, more in the first year than in the second (Fig. 5). In nearby Morro do Japuí, the male NICD ranged from 1 to 5 (mean = 2.3, SD = 1.1, $n = 47$ days). The area covered in these two sites is similar (Fig. 1, see also Freitas 1993).

In Vale do Rio Quilombo, the NICD for males was greater than in Morro do Voturuá (mean = 14.5, SD = 4.1, $n = 12$ days) (Fig. 6A). The area covered in this site was about six times greater than in the previous two, corresponding closely to the NICD ratio for Morro do Japuí (6.3) and suggesting an equivalent density, 40% of that in Morro do Voturuá.

Jolly-Seber analysis for males in Morro do Voturuá (Fig. 7) gave estimated numbers from 3 to 88 individ-

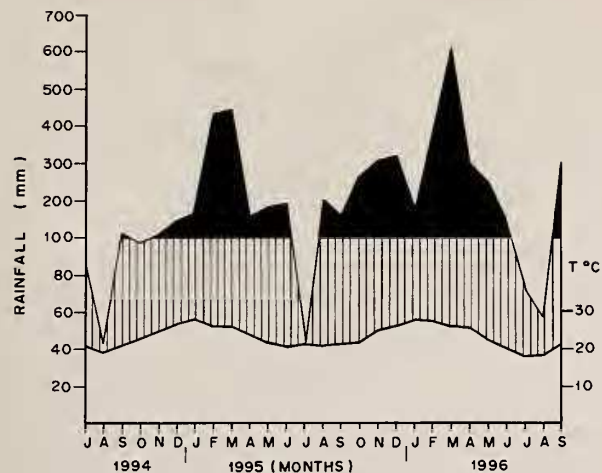


FIG. 2. Climatic diagram of the São Vicente Region during the study period (format following Santos 1965 and Walter 1985). Hatched = humid periods, black = superhumid periods.

uals (mean = 13.5, SD = 9.9, $n = 152$), with most days ($n = 90$) between 10 and 30. The NIPD for males in the same site ranged from 1 to 20 (mean = 9.8, SD = 3.8, $n = 154$). The male population was stable throughout the year, with small fluctuations in number of individuals apparently not related to season, but with lower numbers of individuals observed at the end of winter in the three years (Figs. 4, 5).

The results show that NIPD is better than NICD as an index of population size. In species with stable populations composed of long-lived resident individuals, efficient marking and recapture can give nearly equal population size estimates by the Jolly-Seber method and simple NIPD.

Sex Ratio

The sex ratio of individuals captured and marked was male biased in all sites (Table 1, Figs. 6B and 8). In MV males dominated in all but one month of the study; all the captured individuals were male in four months, including April of both years (Fig. 8). In all, 263 males and 74 females were captured and marked. Males were recaptured from one to 16 times and females from one to five times; 154 males and 30 females were recaptured at least once. The proportion of recaptured males (58.5%) was statistically the same as that of females (40.1%) ($\chi^2 = 2.6$, $df = 1$, $P > 0.20$). In VQ the proportions of recaptures of males (30.8%) and females (30.5%) were equal.

Age Structure

Comparing the new individuals vs. intermediate+old, most of the first captures in MV were of "new" individuals from both males (71%), and females (54%

new), even if this number was considered greater in males ($\chi^2 = 7.6$, $df = 1$, $P < 0.005$). Most of the butterflies captured on each day (after the first) were previously marked individuals (mean = 71.4%, SD = 23.4, $n = 152$ days). The age structure during the 26 months in MV was not stable, with decreases in proportion of "new" individuals in the winter (Fig. 9).

In VQ, the proportion of recaptures/day was high (Fig. 6C), and the age structure quite stable (Fig. 6D), but these results should be taken with care due to the short period of study.

Residence Time

In MV, males had a longer residence time (mean = 37.6 days, SD = 25.8, $n = 154$) than females (mean = 22.6 days, SD = 23.0, $n = 30$) ($t = 2.96$, $df = 182$, $p = 0.004$). Estimated residence time of males ("life expectancy" of Cook et al. 1967) was 28.1 days. The maximum individual permanence (survival) was at least 127 days for a male and 89 days for a female (Table 2). In MJ, residence time was calculated only for males (mean = 18 days, SD = 14.6, $n = 22$), since the recapture rate of females was low (only 3 recaptures). In VQ maximum permanence could not be calculated (due to the short period of study and low number of recaptures), but the residence time for males (mean = 20.1 days, SD = 12.8, $n = 32$) and females (mean = 15.0 days, SD = 10.6, $n = 11$) were not significantly different ($t = 1.17$, $df = 41$, $p = 0.248$).

Vagility

In MV, most adults showed home range behavior, being observed in the same site for several days, often using the same flower resources. The total distance

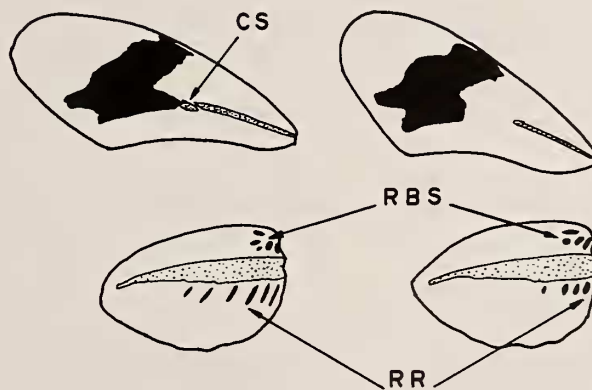


FIG. 3. Wing pattern variation in *Heliconius erato phyllis* (background black, solid = red, dotted = yellow). Colored spot in the inner angle of space Cu1-Cu2 (cubital spot, CS) present (left, red macula almost fused with this), or absent (right). Five basal red spots (RBS) and six red raylets (RR) shaped like small lines (left); four basal red spots and four red raylets shaped like dots (right).

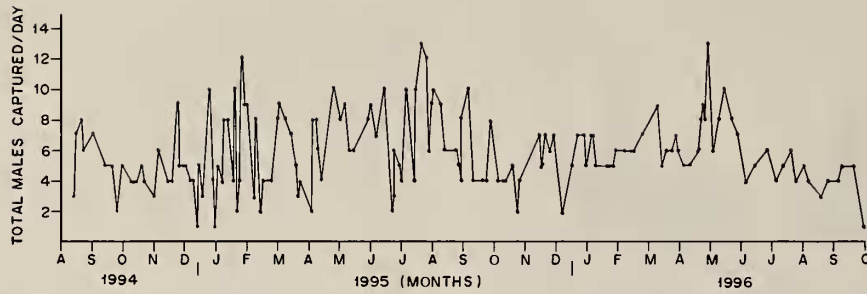


FIG. 4. Daily captures for males of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996.

flown by adults varied among individuals. In general, two classes of individuals could be identified: those always observed in the same site (residents) and those seen in two or more separate points in the study area (vagile). Most of the males (71%) and females (85%) recaptured were vagile, while among the residents, some individuals appeared to have tightly restricted home ranges. One male was captured 17 times (twice on the same day) at the same place, and at least half of the resident individuals were captured more than 4 times. The distance traveled by vagile individuals varied from 50 to 660 m (mean = 270.6, SD = 122.9 m, $n = 97$) for males, and 80 to 600 m (mean = 236.3, SD = 140.9, $n = 23$) for females (Table 3). Some individuals showed great mobility in a single day. In one case, one male captured at 0900 was observed 500 m away at 1000 h, returning at 1030 h to within 50 m of the first site of capture. Males were commonly seen near nectar sources and females were mostly observed near the larval food plants.

Wing Size and Color Pattern in Morro do Voturuá

Four or five red basal spots are present on the ventral hindwing of *Heliconius erato* butterflies. This trait was very stable, as only three out of 337 individuals analyzed (males and females) showed the fifth basal spot (Fig. 3).

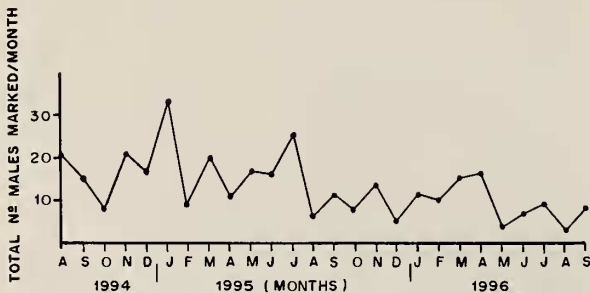


FIG. 5. Monthly recruitment of males of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996, as total number of individuals marked for the first time in each month.

The number of red raylets in butterflies of both sexes showed a bimodal distribution, ranging from one to seven, with peaks at three and five (Table 4). The average number increases in summer and autumn and decreases in winter and spring (Table 4).

The shape of the red raylets varied from a rounded dot to a small red line. Individuals with red raylets shaped like dots (65.8%) were more frequent than those with lines (34.2%). The proportions of each type also varied throughout the year (Fig. 10A).

The cubital spot on the dorsal forewing could be absent, present, or fused with the transverse subapical red bar. If present and not fused, the spot could be red or yellow. This character was very variable, but there was a clear majority of "spot to be present and yellow", with no regular pattern of variation throughout the year (Fig. 10B).

The forewing length of males ranged from 27 to 42 mm, the average varying along the year, with greatest values being observed during the summer (Fig. 11).

The average forewing length of males (mean = 36.25 mm, SD = 2.99, $n = 250$) was greater than that of females (mean = 35.21 cm, SD = 2.96, $n = 71$; $t = 2.58$, $df = 319$, $p = 0.01$). This difference was not found when only recaptured individuals were considered ($t = 1.31$, $df = 181$, $p = 0.191$). When comparing the recaptured vs. not recaptured within sexes, recaptured individuals were smaller. This difference was almost significant for males ($t = 1.933$, $df = 248$, $p = 0.054$), but not for females ($t = -0.172$, $df = 2.83$, $p = 0.864$).

Natural History of Adults

Adults began activity around 0800 h in summer and 0930 h in winter, but this could vary within a season according to the weather. On some cold days during winter, activity began only after 1030 h.

Beak marks (from handling and release by, or escape from, bird predators) were found on the wings of individuals from all populations, but a different proportion of individuals with damaged wings was ob-

TABLE 1. Sex ratio of marked individuals of *H. erato phyllis* in the three study sites.

Study site	Males	Females	Sex ratio	χ^2 values
Morro do Voturuá	263	74	3.5:1	105.9
Morro do Japuí	50	6	8.3:1	34.6
Vale do Rio Quilombo	104	36	3:1	33

served in each site. Beak marks were seen in MV on 18 males (6.8%; 14 later recaptured) and 1 female (1.3%); in MJ, on 10 males (20%) and no females; in VQ, on 18 males (17%) and 8 females (22%).

Adults were almost always observed feeding on flowers, but a few individuals were observed feeding on damaged fruits of *Rubus rosaefolius* Smith (Rosaceae), and in one case a captured individual was observed bearing a seed of this plant on its proboscis. The most visited flower in the MV site was *Lantana camara* L. (Verbenaceae) (more than 150 records). Two varieties of *L. camara* occur in the study area, one with red-yellow flowers and the other (much more common) with white flowers. Some individuals were also observed visiting flowers of *Rubus rosaefolius* (30 records), *Asclepias curassavica* L. (Asclepiadaceae) (13 records), *Epidendrum fulgens* Brongn. (Orchidaceae) (3 records), *Gurania* sp. (Cucurbitaceae) (3 records), and *Impatiens walleriana* Hook. f. (Balsaminaceae) (2 records). Pollinia of *Epidendrum fulgens* and *Asclepias curassavica* were observed attached to the proboscis of some captured individuals. A new male was once observed visiting the inflorescence of *Heliconia* sp. (Musaceae). Individuals in MV were rarely observed feeding on flowers of Asteraceae, although several species of *Mikania*, *Eupatorium*, and *Vernonia* are common there. The few Asteraceae that were observed being visited include *Mikania lundiana* D.C. (3 records), *Trixis antimenorrhoea* Mart. ex. Baker (3 records), *Eupatorium laevigatum* D.C. (3 records), and *Emilia sonchifolia* D.C. (2 records). In the VQ site (where *L. camara* is not so common), the Asteraceae *Bidens pilosa* L. and *Tithonia speciosa* Hook ex Gris. were the most visited species with 90 and 45 feeding records respectively. Also in this site *Stachytarpheta polyura* (L.) (Verbenaceae) was commonly used (15 records). Some adults in MV appeared to show "trap-line" (learned sequence) behavior for gathering pollen and nectar (see Ehrlich & Gilbert 1973 and Ehrlich 1984).

Over a two-month period, one male was observed visiting a dense *Lantana* patch at about 1000 h, and then in another patch 150 m away after 30–40 minutes. Several individuals showed similar patterns throughout the two years of study. Occasional disturbance on forest edges (removal of some flower patches)

TABLE 2. Permanence of marked *H. erato phyllis* in the "Morro do Voturuá". Days elapsed between marking and last recapture represent the minimum permanence (MP) for each individual.

MP	Males	P(%)	Females	P(%)	Total
1–20	51	33.1	18	60.0	69
21–40	38	24.7	5	16.7	43
41–60	34	22.0	5	16.7	39
61–80	21	13.6	1	3.3	22
81–100	9	6.0	1	3.3	10
>100	1	0.6	0	0.0	1
Total	154	100.0	30	100.0	184

resulted in disappearance of some individuals from the study area for up to two weeks.

Four *Passiflora* species were recorded as larval food-plants in MV: *Passiflora alata* Dryand, *P. edulis* Sims (both used rarely), *P. jileki* Wawra, and *P. capsularis* L. Other species may be used in the same area and in the neighboring sites. The behaviors observed in ovipositing females and larvae were the same as reported in the literature (see Brown 1981).

DISCUSSION

Populational Ecology and Adult Biology

The population parameters of *H. erato phyllis* seen in this study agree with those reported for other tropical *Heliconius* (Turner 1971, Ehrlich & Gilbert 1973, Araujo 1980, Mallet & Jackson 1980, Ehrlich 1984, Mallet et al. 1987, Quintero 1988). The MV population was reasonably stable in numbers during the two years of study if compared with species of other sub-families such as Ithomiinae and Troidini, both showing pronounced fluctuations in numbers through time (Vasconcellos-Neto 1980, Brown et al. 1981, Francini 1989, Freitas 1993, 1996, Tyler et al. 1994, Pinto & Motta 1997). Other features observed for *H. erato* in the present study were the continual recruitment of new individuals, low density of adults, absence of sudden increases and decreases in numbers of individuals, and non-cyclical age structure. The population seems to be less affected by climate than those observed by Benson (1978) for populations in a drier site in Rio de Janeiro or Saalfeld and Araujo (1981) for populations

TABLE 3. Maximum distance (m) traveled by adults of *H. erato phyllis* in MV.

	Residents		Vagile	
	up to 50	51–150	150–500	>500
Males	39	17	77	3
Females	4	8	13	2
Total	43	25	90	5

TABLE 4. Frequency distributions, sample size (N), mean (X), and standard deviation (SD) of the number of "red raylets" for month of first capture in butterflies of both sexes captured in the "Morro do Voturuá".

Month/year	Number of Red raylets							N	X ± SD
	1	2	3	4	5	6	7		
Aug/1994	2	5	2	8	2	1	0	20	3.3 ± 1.4
Sep/1994	0	3	6	4	2	0	0	15	3.3 ± 1.0
Winter/1994	2	8	8	12	4	1	0	35	3.3 ± 1.2
Oct/1994	0	0	4	1	3	0	0	8	3.9 ± 1.0
Nov/1994	0	2	6	6	4	3	0	21	4.0 ± 1.2
Dec/1994	0	2	7	2	5	1	0	17	3.7 ± 1.2
Spring/1994	0	4	17	9	12	4	0	46	3.9 ± 1.2
Jan/1995	0	4	8	5	10	6	0	33	4.2 ± 1.3
Feb/1995	1	0	0	1	2	5	0	9	5.0 ± 1.6
Mar/1995	1	0	3	4	8	3	1	20	4.5 ± 1.4
Summer/1995	2	4	11	10	20	14	1	62	4.4 ± 1.4
Apr/1995	0	0	1	0	5	3	1	9	5.3 ± 1.1
May/1995	1	2	3	3	8	0	0	17	3.9 ± 1.3
Jun/1995	0	2	3	4	5	2	0	16	4.1 ± 1.3
Autumn/1995	1	4	7	7	18	5	1	43	4.3 ± 1.3
Jul/1995	2	4	9	4	5	1	0	25	3.4 ± 1.3
Aug/1995	2	0	1	1	1	1	0	6	3.3 ± 2.1
Sep/1995	2	2	5	1	1	0	0	11	2.7 ± 1.2
Winter/1995	6	6	15	6	7	2	0	42	3.2 ± 1.4
Oct/1995	0	2	3	1	0	2	0	8	3.6 ± 1.6
Nov/1995	1	1	3	6	1	1	0	13	3.6 ± 1.6
Dec/1995	0	2	1	0	1	1	0	5	3.6 ± 1.8
Spring/1995	1	5	7	7	2	4	0	26	3.6 ± 1.4
Jan/1996	0	2	1	1	5	2	0	11	4.4 ± 1.4
Feb/1996	0	0	1	0	4	5	0	10	5.3 ± 1.0
Mar/1996	0	1	4	0	5	5	0	15	4.6 ± 1.4
Summer/1996	0	3	6	1	14	12	0	36	4.7 ± 1.3
Apr/1996	0	0	2	3	4	6	1	16	5.1 ± 1.2
May/1996	0	1	1	0	1	1	0	4	4.0 ± 1.2
Jun/1996	0	1	2	1	2	1	0	7	4.0 ± 1.4
Autumn/1996	0	2	5	4	7	8	1	27	4.6 ± 1.4
Jul/1996	1	3	2	1	2	0	0	9	3.0 ± 1.5
Aug/1996	0	1	0	0	0	2	0	3	4.7 ± 2.3
Sep/1996	2	3	3	0	0	0	0	8	2.2 ± 0.8
Winter/1996	3	7	5	1	2	2	0	20	2.9 ± 1.5
Total	15	43	81	57	86	52	3	337	3.9 ± 1.4

much farther south. In the latter populations, three distinct phases were reported: a period of rapid growth in early spring, a period of maximum density in summer through autumn, and an abrupt decline in winter (Saalfeld & Araujo 1981, Romanowsky et al. 1985). In the periods of maximum density, the number of individuals captured in these populations could be very high (more than 150 individuals reported in one roosting site) in relation to the maximum values obtained in the present study (from 20 to 30 individuals) (Saalfeld & Araujo 1981, Romanowsky et al. 1985).

The average time of residence and the life expectancy reported in the present study are both high, like those of other *Heliconius* (Turner 1971, Benson 1972, Ehrlich & Gilbert 1973, Araujo 1980, Quintero 1988), including the populations from southern Brazil (Romanowsky et al. 1985). The values are higher than those of many Ithomiinae, Pieridae, and Papilionidae

in the same or nearby sites (Table 5; see also Young & Moffett 1979, Vasconcellos-Neto 1980, Brown et al. 1981, Freitas 1993, 1996, Tyler et al. 1994, Pinto & Motta 1997). The high values for residence are not related to geographic location of the populations, since they are higher in *Heliconius erato* than in butterflies of other groups in the same and nearby sites (Table 5).

In part the high values of residence reported in *Heliconius* could be related to the movements and dispersal of the adults. Some *Heliconius* and *Eueides* butterflies are known to have restricted home ranges throughout their lives, and even if adults can fly distances up to 5 km within the forest (Brown 1981, Pansera & Araujo 1983, Romanowsky et al. 1985, Mallet et al. 1987), small areas of open field could act as efficient barriers to dispersal (Romanowsky et al. 1985). This pattern contrasts with that of "nomadic" butterflies such as Ithomiinae and Troidini (see discus-

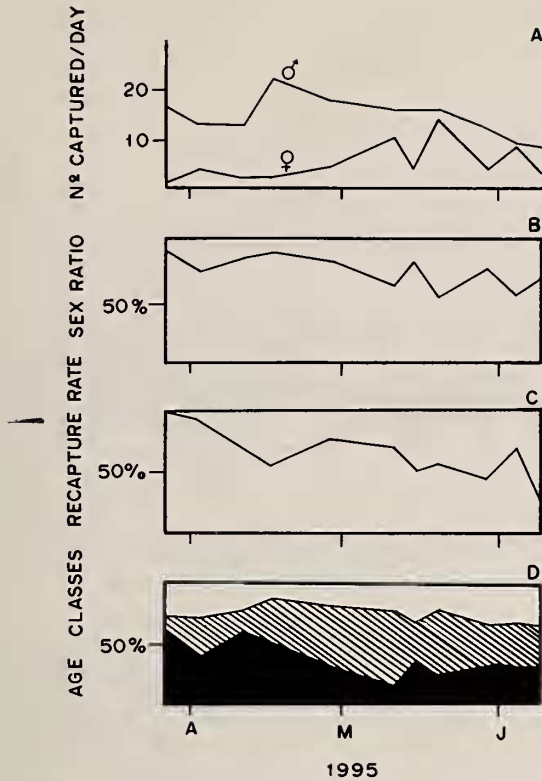


FIG. 6. Populational parameters of *H. erato phyllis* in Vale do Rio Quilombo, March to June 1995. A, daily captures of males (top line) and females; B, sex ratio as percent of males in each day's captures; C, percent of captures of males; D, age structure of males as in Fig. 4.

sion in Mallet et al. 1987) and probably other more primitive genera of Heliconiini like *Dryas*, *Agraulis* and *Dione* (K. Brown, pers. comm.). For example, although some Ithomiinae are reported to live as long as 10 months (e.g., *Mcclungia salonina* (Hewitson), R. S.

C. Dias & K. S. Brown, pers. comm.), several studies showed low rates of recapture and low permanence values for species in this subfamily, probably as a result of the high dispersal of the individuals (Gilbert 1993). But even if movement explains in part the residence values of adults, almost certainly the high actual longevity of the adults is the main factor affecting this parameter in *Heliconius*.

In the present study, sex ratio was male biased; several previous field studies reported male biased sex ratios even when the sex ratio in the laboratory was 1:1 (Ehrlich & Gilbert 1973, Mallet & Jackson 1980, Ehrlich 1984, Ehrlich et al. 1984, Freitas 1993). This difference in capture between sexes may be due to differential behavior of the adults, with males generally flying in the same places as the collectors, and females more dispersed throughout the habitat looking for host plants (Freitas 1996).

Contrasting with these features, which agree with those found in other species of *Heliconius*, the use of food resources by *H. erato phyllis* in the São Vicente region is unlike that of many other tropical species of the same genus. The butterflies seem to prefer feeding along forest edges on common second-growth flowers, even though a species of Rubiaceae and *Gurania* sp. (Cucurbitaceae) flowers are common in clearings in the forests, where they are heavily used by *Heliconius numata robigus* Weymer. It is interesting that sympatric *H. sara apseudes* (Hübner) and *H. ethilla narcaea* (Godart) have flower preferences similar to those of *H. erato phyllis* (pers. obs.), perhaps related to their specialization on small pollen grains (Boggs et al. 1981) and the use of larval host plant species typical of successional habitats (Gilbert 1991).

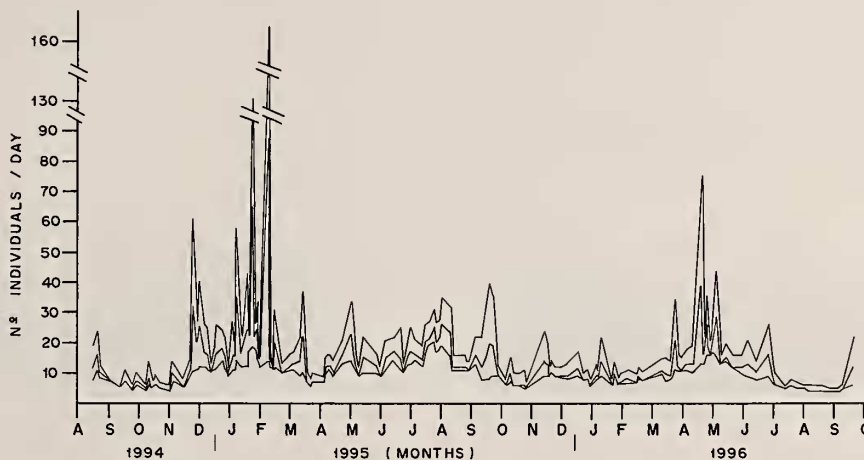


FIG. 7. Estimated population size (Jolly-Seber) for *H. erato phyllis* (males) in Morro do Voturuá, August 1994 to September 1996 (middle). The maximum number of individuals is given as the estimate plus the error (top line), and the minimum number is given as the NIPD (bottom line), assuming that the population could not be lower than this number (see also Freitas 1993, 1996).

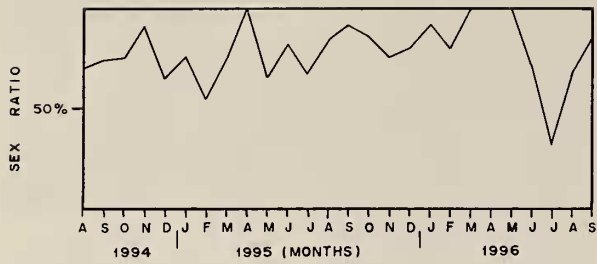


FIG. 8. Sex ratio for *H. erato phyllis* marked in Morro do Voturuá, August 1994 to September 1996 (based on monthly recruitment), as percent of males in each month's captures.

Wing Color Pattern

Although the number of red basal spots is relatively constant in this population of *H. erato phyllis*, other elements of color pattern are not: the number of "red raylets" varies seasonally, and the shape of the red raylets and the cubital spot on the dorsal forewing vary during the year with no clear pattern. The number and shape of the basal spots on the ventral hindwing is one of the distinctive characters used in *Heliconius* classification. This character was discussed by Emsley (1965) as probably important in courtship as a recognition mechanism. If this is true, the constancy of this character is easily explained.

The pattern observed in the shape of the red raylets and in the cubital spot is not easy to explain, but random variation is the most probable hypothesis. There are no known pressures acting on these two characters.

Oliveira and Araujo (1992) proposed that the mean number of red raylets is related to temperature: the hot months should have a high proportion of individuals with numerous red raylets. The genetic determination of this character was defined by Pansera and Araujo (1983), but numeric polyphenism could not be discarded. Polyphenism occurs in several species in seasonal environments (Brakefield & Larsen 1984, Braby 1994, Windig et al. 1994). In southern Brazil (30°S), adult populations greatly decline during the

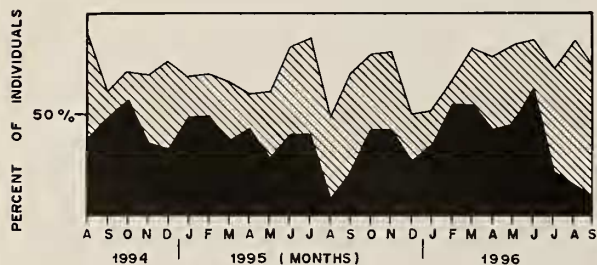


FIG. 9. Age structure for male *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996 (black = fresh individuals, hatched = intermediate, white = worn individuals as % of each day's captures).

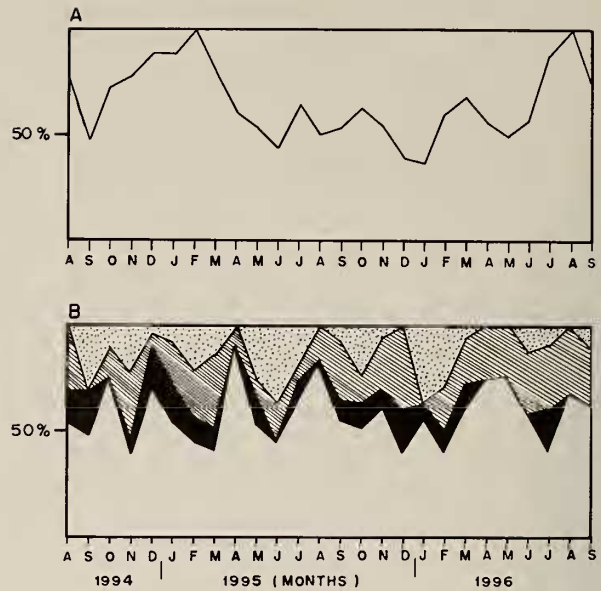


FIG. 10. Monthly variation of two wing pattern elements in adults of both sexes of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996. A, ratio between red raylets of both shapes as percentage of individuals with red raylets shaped like dots. B, ratio among the four different phenotypes of the colored spot in the inner angle of space Cu1-Cu2: white = present yellow, black = present red, hatched = absent, dotted = fused with the subapical red macula.

cold winter, and the variation in the number of red raylets could be explained through the resulting bottlenecks (A. M. Araujo, pers. comm.). In the São Vicente region (24°S), low temperature does not kill adults in winter, and genes are not eliminated in this way. Although color pattern frequencies are not stable, the population itself shows a relative stability in number throughout the year, indicating that this variation occurs without reduction in population size, suggesting that the variation could be due to simple numerical polyphenism.

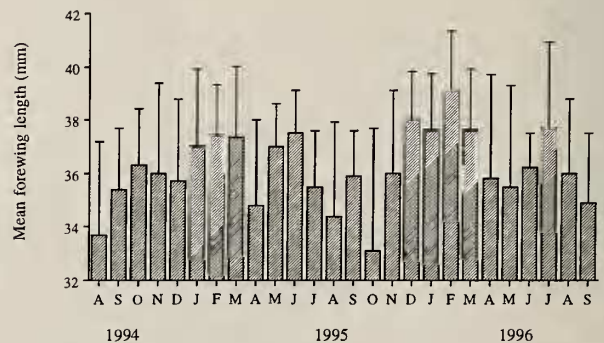


FIG. 11. Mean forewing length of males of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996 (based on monthly recruitment). Histogram bars = monthly means, line extensions = standard deviation.

TABLE 5. Residence values (in days) for some butterfly species in Southeastern Brazil. Mean mr = mean minimum residence, mo = maximum for one individual.

	Males		Females	
	mean mr	mo	mean mr	mo
São Vicente Region				
Nymphalidae				
<i>Heliconius erato phyllis</i> ¹ Morro do Voturuá	37.6 ± 25.8	127	22.6 ± 23.0	89
<i>Heliconius erato phyllis</i> ¹ Morro do Japuí	18.04 ± 14.6	47	—	22
<i>Melinara ludovica paraiya</i> Reakirt ²	14.1 ± 14.1	55	—	—
<i>Melinara ethra</i> Godart ²	13.7 ± 12.9	47	—	—
<i>Placidula eurjanassa</i> ^{2,3}	8.4 ± 8.3	45	7.2 ± 5.7	23
<i>Mechanitis lysimnia lysimnia</i> Fabricius ²	15.5 ± 15.4	67	18.3 ± 16.2	72
<i>Dircenna dero celtina</i> Burmeister ²	9.4 ± 6.9	23	10.9 ± 10.5	49
<i>Heterosais edessa</i> Hewitson ²	12.9 ± 15.1	65	13.5 ± 10.3	39
<i>Hypothyris ninonia daeta</i> (Boisduval) ⁴	16.3 ± 11.1	40	14.2 ± 16.2	52
<i>Pseudoscada erruca</i> (Hewitson) ⁴	9.9 ± 9.6	25	—	33
<i>Ithomia drymo</i> Hübner ⁴	7.0 ± 7.3	17	12.3 ± 12.1	26
<i>Actinote pellenea pellenea</i> Hübner ⁵	3.2 ± 2.6	12	—	6
<i>Actinote brylla</i> Oberthür ⁵	—	16	—	16
Papilionidae				
<i>Parides anchises nephalion</i> Godart ⁶	14.1 ± 8.2	30	9.0 ± 3.6	12
Other regions				
Nymphalidae				
<i>Heliconius erato phyllis</i> ⁷	30.7 ± 29.0	112	—	—
<i>Aeria olena olena</i> Weymer ⁸	8.7 ± 5.9	24	11.7 ± 2.5	14
<i>Actinote zikani</i> D'Almeida ⁹	3.9 ± 1.3	7	—	—
<i>Pierella lamia</i> Sulzer ¹⁰	—	60	—	—
Pieridae				
<i>Eurema elathea</i> (Cramer) ¹¹ dry season	10.9 ± 9.1	52	9.7 ± 9.8	54
<i>Eurema elathea</i> ¹¹ wet season	8.8 ± 5.6	28	6.9 ± 4.2	21

Superscript numbers : 1, this study; 2, Freitas 1996; 3, Freitas 1993; 4, Freitas, unpubl. data from Morro do Japuí; 5, Francini 1989; 6, Freitas, unpubl. data from Morro do Voturuá; 7, Francini, unpubl. data from Lavras, MG, Brazil; 8, Vanini and Freitas, unpubl. data from Campinas, SP; 9, Francini, unpubl. data from Paranaipicaba, SP; 10, Freitas, unpubl. data from Sete Barras, SP; 11 Vanini, Bonato and Freitas, unpubl. results from Campinas, SP.

Ecological Plasticity in *Heliconius*?

Several features of *H. erato* vary in different parts of the neotropics. Although in the São Vicente region and Trinidad the populations are stable, maintaining constant low numbers throughout time (Turner 1971, R. B. Francini, pers. obs.; this study), in southern Brazil they show strong fluctuations over the year, with some extinction in colder years (Saalfeld & Araujo 1981, Romanowsky et al. 1985). *Heliconius erato* is reported as feeding on more than 37 species and 6 genera/subgenera of Passifloraceae (Benson et al. 1976, Brown 1981, Spencer 1988), even using *Passiflora edulis* and *P. alata*, host species normally rejected in most populations, on forest edges and urban areas (this study, A. V. L. Freitas, pers. obs., and unpublished results by L. S. Otero and K. S. Brown Jr.). The differences in use of flower resources among areas in this study shows that *H. erato phyllis* rapidly responds to variations in resource availability in different sites and seasons.

Heliconius erato, especially the subspecies *phyllis*, seems to be able to persist in many kinds of climate

and vegetation. Colonies of this subspecies are present in virtually any kind of vegetation in southeastern and southern Brazil, including primary and secondary forest edges, urban parks, plantations of *Pinus* and *Eucalyptus*, riparian forests, savannas and sandy soil forests, and in tropical, subtropical, and temperate environments (Araujo 1980 and pers. obs. of the authors). This is probably related to the ability of this species (especially the subspecies *phyllis*) to use a great range of larval and adult resources, and change behavior and preferences according to the environment (=ecological plasticity).

Such statements could apply not only to *H. erato*, but also to *H. sara* and *H. ethilla* populations in southeastern and southern Brazil, both with similar generalist habits, and could help to explain patterns of distribution of the species of this genus. In contrast to the three species cited above, four other *Heliconius* of southeastern Brazil have much more restricted habits. *Heliconius melpomene nanna* Stichel, *H. numata robigus* and *H. nattereri* Felder & Felder, are restricted to limited sectors of forest habitats, the last one with a

very small range, a poor competitor with *H. sara* and other lowland species (Brown 1972, W. W. Benson, pers. comm.); *H. besckei* Ménétriés (a co-mimic of *H. erato*) is typical of Atlantic forest mountains, in primary and secondary forests at medium high altitudes, descending to sea level only in winter (Brown & Mielke 1972 and unpublished results by the authors).

Even though environmental tolerance may help explain distributions of the species of *Heliconius*, other factors need to be investigated. Benson (1978) argues that the availability of new host plant shoots in the dry winter results in high competition and is responsible for the absence of *H. melpomene* in a seasonal site in South Brazil. In the São Vicente region, however, this seasonality is much less pronounced, and periods of severe drought are virtually absent (Fig. 2); new shoots of *Passiflora* species seem to be abundant throughout the year, and though a detailed study needs to be carried out, this could not explain the absence of *H. melpomene* south of Rio de Janeiro State. Although these ideas and many others were discussed by Gilbert (1984), there still seem to be more questions than answers.

Population studies need to be undertaken with other species of Heliconiini, especially the more widespread species of *Heliconius*, such as *H. ethilla* and *H. sara*. The presence of seasonal polyphenism may indicate species with broad tolerances to different environments, as has been suggested for other polyphenic butterflies (Shapiro 1976, Kingsolver & Wiernasz 1991, Van Dyck et al. 1997), although in *Heliconius* this could be apparently without adaptive consequences. These studies could guide future research in population biology of butterflies, and help in the understanding of the ecology of tropical insects.

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